

**HYPOGEAL MARGARODIDS OF THE GENUS *HETEROMARGARODES*  
JAKUBSKI (HEMIPTERA: MARGARODIDAE) FROM THE WESTERN  
UNITED STATES**

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*Abstract.*—Soil-dwelling scale insects with cystlike feeding stages, called ground pearls, belong to several genera of Margarodidae (Hemiptera: Coccoidea), including *Heteromargarodes* Jakubski known only from the western United States. We revise and redescribe *Heteromargarodes* and its type species, *H. americanus* Jakubski, based on the adult female. In addition, *Margarodes chukar* McDaniel and *Margarodes hiemalis* Cockerell are transferred to *Heteromargarodes* as *H. chukar* (McDaniel), **new combination**, and *H. hiemalis* (Cockerell), **new combination**, respectively, and redescribed based on the adult female. A lectotype is designated for *M. hiemalis*. Another North American ground-pearl species, *Margarodes dactyloides* McDaniel, is found to be a **new synonym** of *Eumargarodes laingi* Jakubski. A key to the genera of ground pearls found in North America is included.

*Key Words:* Scale insects, ground pearls, hypogeal insects, taxonomy

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The hypogeal margarodids, also called ground pearls, have been treated as the tribe Margarodini of the Margarodidae *sensu lato* by Morrison (1928), as part of the subfamily Margarodinae (Ben-Dov 2005), as two families, Margarodidae *sensu stricto* and Termitococcidae, by Jakubski (1965), and as one family, Margarodidae *sensu stricto* by Koteja (2001), Foldi (2005), and Hodgson and Foldi (2006). This group is considered to comprise the following ten genera: *Dimargarodes* Silvestri, *Eumargarodes* Jakubski, *Eurhizococcus* Silvestri, *Heteromargarodes* Jakubski, *Margarodes* Guilding, *Margarodesia* Foldi, *Neomargarodes* Green, *Porphyrophora* Brandt, *Promargarodes* Silvestri, and *Termitococcus* Silvestri (Ben-Dov 2005). In Jakubski's (1965) taxonomic monograph, he described the immature and adult fe-

males of all species known at that time, but he illustrated only the spiracles and pores. His generic concepts are difficult to apply, some genera may be synonyms, and his subfamily and tribal classification appears to be artificial. Foldi (2001) listed a total of 107 species of hypogeal margarodids belonging to the above genera, including a number of recently described species from Kazakhstan, Turkmenistan, Mongolia (e.g., Jashenko 1989, 1990, 1994) and China (Tang and Hao 1995, Tang 2000). The genus *Porphyrophora* has been revised recently for species from Europe, the Middle East and North Africa (Vahedi 2002, Vahedi and Hodgson in press) and the South African species of *Margarodes* have been revised by De Klerk (1982) and De Klerk et al. (1982, 1983). However, there appears to be much convergence in

morphology among genera, it is not clear which morphological characters are informative phylogenetically, and there have been no molecular phylogenetic studies to provide data for re-interpreting morphological taxon concepts.

The name ground pearls derives from the cystlike nymphs which are very reduced in morphology and live underground on the roots of their host plants, protected inside a membranous or hardened covering that is frequently pearly in appearance (Morrison 1928, Jakubski 1965). The life cycles of most species of ground pearls have not been studied, however most species are considered to have just three instars in the female: first, second (cyst stage) and adult (Jakubski 1965, Danzig 1980), although Foldi (2005) suggested that up to three cyst stages may occur, depending on species. A number of species are injurious to their host plants, often grasses, attacking turf grass in parts of the U.S.A. (Hoffman and Smith 1991, Gill 1993), sugar cane in Australia (Dominiak et al. 1989), and grape vines in South Africa and South America (De Klerk et al. 1982, Foldi and Soria 1989). The centipede grass ground pearl, *Dimargarodes meridionalis* (Morrison), is known to infest the roots of both grape vines and a range of grasses in the southwestern and southeastern United States (Barnes et al. 1954, Ebeling 1959, Kouskolekas and Self 1974, Gill 1993).

The biology of North American pestiferous ground pearls has been reviewed by Kouskolekas and Self (1974) and Hoffman and Smith (1991). These species overwinter as cysts and females mature in late spring to mid summer and emerge from the cyst. In sexual species the adults mate, and the adult females produce and deposit their eggs in an ovisac at the roots of the host plants before autumn. There is usually one generation per year, but there can be as many as three (Baker 1982). If conditions

are not favorable for emergence, the overwintering cysts may remain in that stage for several years (Brandenberg 1995) with the record reported for cyst dormancy being 17 years in *Margarodes vitis* (Philippi) (Ferris 1919). In Australia, the ground pearl *Eumargarodes laingi* Jakubski is univoltine and adult females emerge beginning in spring and continue to emerge through the summer months (Allsopp and McGill 1997, Samson and Harris 1998).

Five genera—*Dimargarodes*, *Eumargarodes*, *Heteromargarodes*, *Margarodes*, and *Promargarodes*—and a total of nine species of hypogeal margarodids have been recorded from North America (Jakubski 1965; McDaniel 1965, 1966), but few have been described by modern standards and the most comprehensive key (McDaniel 1966) dealt with only five species. The monotypic genus *Eumargarodes* has been recorded from the southeastern United States but is also a pest in Australia (Jakubski 1965) and is believed to be native to North America (Jakubski 1965). *Heteromargarodes* was described for *H. americanus* Jakubski, known only from Wyoming with no recorded host plant (Jakubski 1965), and was redescribed by Foldi (2005) based on one adult female that he designated as the lectotype. Until recently, most other North American species of hypogeal margarodids have been treated as members of *Margarodes* (Foldi 2001; Ben-Dov 2005), although this generic placement is uncertain. Jakubski (1965) transferred *Margarodes hiemalis* Cockerell to *Porphyrophora*, although it is not clear why as he did not list any specimens he examined. He also transferred *Margarodes meridionalis* to *Dimargarodes* apparently based on pore characteristics of the adult female. The recent catalogue of Margarodidae (Ben-Dov 2005) followed Jakubski's placement of these two species, and also transferred *Promargarodes floridanus* Jakubski to *Margarodes* fol-

lowing Vahedi (2002). The placement of *M. meridionalis* in *Dimargarodes* appears to be justified, but the justification for the other two transfers is unclear. Thus below, we continue to refer to these two species by their most widely used combinations, i.e., *M. hiemalis* and *P. floridanus*. The nine ground-pearl species known to occur in the U.S.A. are distributed as follows: *D. meridionalis* in southern U.S.A., Arizona, and California (Barnes et al. 1954, Ebeling 1959, Gill 1993), *E. laingi* found only in the southeastern states (Spink and Dogger 1961, Jakubski 1965), *H. americanus* in Wyoming (Jakubski 1965), *M. chukar* La Rivers in Nevada (La Rivers 1967), *M. dactyloides* McDaniel and *M. morrisoni* McDaniel in Texas (McDaniel 1965), *M. hiemalis* in New Mexico (Cockerell 1899), *M. rileyi* Giard in Florida and the Caribbean (Jakubski 1965), and *P. floridanus* (Jakubski) in Florida (Giard 1894, Morrison 1927, Jakubski 1965).

We revise the genus *Heteromargarodes*, which is here considered to comprise three species. *Margarodes chukar* and *M. hiemalis* are transferred to *Heteromargarodes* as *H. chukar*, new combination, and *H. hiemalis*, new combination, respectively, based on examination of the type specimens. We provide a revised description of the genus and a description of each species based on the adult females, as well as a diagnosis of the cyst stage. In addition, *M. dactyloides* is synonymized with *E. laingi* based on study of the newly rediscovered holotype of *M. dactyloides*. We include a key to all genera of ground pearls found in North America.

#### MATERIALS AND METHODS

All material studied consisted of slide-mounted museum specimens, a few of which were remounted using a method adapted from Kozarzhevskaya (1986) and described in Gullan (1984). Specimens are deposited in the Australian

National Insect Collection, CSIRO, Canberra (ANIC); the Bohart Museum of Entomology, University of California, Davis (BME); The Natural History Museum, London (BMNH); the California State Collection of Arthropods (CSCA), Plant Pest Diagnostics Branch, California Department of Food and Agriculture (CDFA), Sacramento; and the National Entomological Collection of the National Museum of Natural History, housed in Beltsville, Maryland (USNM). One adult female specimen (♀) is mounted on each slide, unless otherwise stated.

The morphological terms of Jakubski (1965) and Vahedi (2002) are used with some modifications. Setae are distinguished from spines by the presence of a basal collar by which each seta articulates with the cuticle. Spines lack this feature. Body setae in *Heteromargarodes* are of two types: long hairlike setae arranged in segmental bands, and short hairlike setae scattered amongst the long setae, and especially numerous near the ventral midline. Antennae have coeloconic sensilla (Koteja 1980), short hairlike setae, long hairlike setae (also called flagellate setae) and fleshy setae; the latter are stouter than hairlike setae and have blunt apices. The trochanter of each leg has campaniform sensilla, which are small, clear, oval pores that may or may not have sensory function. Similar structures to these are found on the derm outside the opening of the thoracic spiracles. These are called perispiracular pores and their function is not known. Pores found on the ventral and dorsal surface of the derm are called multilocular pores because they each contain several to many circular loculi (openings). The multilocular pores of *Heteromargarodes* do not have a distinct outer rim of small loculi, as found in many other ground-pearl genera, and are referred to here as sievelike multilocular pores. Measurements are expressed as

the range and are given in millimeters (mm) and in micrometers (µm). The enlargements are not drawn to the same scale as each other. The measurements and figures of the adult female of *H. chukar* are based only on the type material, whereas for *H. hiemalis* measurements from the holotype and another specimen were included, and for *H. americanus* measurements from the lectotype and seven other specimens were included. The generic description of the cyst stage is based on the paralectotype of *H. americanus* and on material of *H. hiemalis* from Santa Rita Experimental Station, Arizona.

KEY TO GENERA OF NORTH AMERICAN GROUND PEARLS BASED ON SLIDE-MOUNTED ADULT FEMALES (NOTE THAT THIS KEY WILL NOT WORK IN OTHER REGIONS.)

- 1 Spines absent from derm. Dorsal pores without outer rim of small loculi; each pore with either multilocular or sievelike center . . . . . 2
- Spines present on derm. Dorsal pores with rim of small loculi; each pore with either bi- or multilocular center. . . . . 3
- 2(1) Abdominal cuticle without raised bare patches of cuticle. Abdominal spiracles in 3 pairs. Setae on legs robust, spinelike, with large collars. Dorsal pores each with 4-8 loculi in central circle . . . . . *Eumargarodes* Jakubski
- Abdominal cuticle with raised bare patches of cuticle. Abdominal spiracles in 6 pairs. Setae on legs hairlike, similar to setae on cuticle. Dorsal pores sievelike, each with 10-30 loculi . . . . . *Heteromargarodes* Jakubski
- 3(1) Derm pores with distinct bilocular center . . . . . *Dimargarodes* Silvestri
- Derm pores with multilocular center . . . . . 4
- 4(3) Abdominal spiracles in 6 pairs. Cicatrices absent on venter of abdomen. Apices of spines on cuticle always pointed . . . . . *Promargarodes* Silvestri
- Abdominal spiracles in 5 or 7 pairs. Cicatrices present or absent on venter of abdomen. Apices of spines on cuticle rounded, or pointed . . . . . *Margarodes* Guilding

*Heteromargarodes* Jakubski

*Heteromargarodes* Jakubski 1965. Type species: *Heteromargarodes americanus* Jakubski 1965, by original designation and monotypy.

Description.—*Adult female*: Body oval, 3.8-10.9 mm long, 3.0-10.0 mm wide, abdomen with 9 segments; abdominal segment I represented ventrally by a small area lateral to metathoracic leg; apex of abdomen with or without a membranous, setose projection or boss. Derm with dense papillae (each 7-12 µm across) over entire body. Eyes absent. Antenna 8-segmented, segments II and III partially fused giving a 7-segmented appearance; segment I longest and widest with papillose derm and 3-7 hairlike setae 15-124 µm (mostly <35) long; segments II and III almost bare, each with 0-5 short hairlike setae, 15-25 µm long; segments IV-VIII cylindrical, with apical segment (VIII) narrowest, 60-110 µm long, 40-110 µm wide; sensilla and setae of segments IV-VIII as follows (many setae broken and missing and number often unreliable): flagellate setae each 40-250 µm long: 1-5 on IV, 3-7 on V, 3-8 on VI, 4-8 on VII and 8-12 on VIII; long fleshy setae (10-30 µm long): 1 or 2 on IV, 2-4 on V, 5-7 on VI, 4-6 on VII and 8-16 on VIII; short fleshy setae: probably 1 or 2 on VIII (difficult to see); coeloconic sensilla (not illustrated) 1-3 on at least each of segments IV-VI (difficult to see). Mouthparts absent, represented only by cuticular folds. Prothoracic legs fossorial, much larger than mesothoracic and metathoracic legs; base of coxa with 10-12 short setae each 10-15 µm long; trochanter + femur 350-1000 µm long, 400-800 µm in basal width; tibia and tarsus 360-1025 µm long; sclerotized claw 380-650 µm long, without denticle; trochanter with 7-9 campaniform sensilla on each side; femur with hairlike setae (80-250 µm long), most numerous anteroventrally, and

scattered short hairlike setae (15–30  $\mu\text{m}$  long); tibia and tarsus with a group of setae (60–100  $\mu\text{m}$  long) present antero-ventrally. Mesothoracic and metathoracic legs similar in structure to prothoracic legs, but smaller and narrower; base of each coxa 350–750  $\mu\text{m}$  wide with short setae (10–15  $\mu\text{m}$  long) and long setae (200–500  $\mu\text{m}$  long) ventromedially; trochanter + femur 150–300  $\mu\text{m}$  long, 200–500  $\mu\text{m}$  in basal width; tibia plus tarsus 200–350  $\mu\text{m}$  long; sclerotized claw 200–300  $\mu\text{m}$  long, almost straight, without denticle; trochanter narrow with 4–7 campaniform sensilla on each side, without hairlike setae; femur sparsely covered with short setae dorsally and laterally and group of long setae ventrally; tibia partially fused with tarsus, covered with short setae dorsally and laterally, several long setae ventrally; tarsus completely fused with claw, with a trace of suture all round, 3 or 4 long (80–100  $\mu\text{m}$ ) ventral setae. Anal area at posterior end of body, dorsally on segment IX; anal opening circular on an elliptical sclerotized area; anal tube simple, with simple sclerotized anal ring and lateral apodemes. Thoracic spiracles large, ovalshaped, well chitinized; atrium of each peritreme with numerous sievelike multilocular pores in 1–2 dense rows, similar in structure to pores found on derm, each pore 12–16  $\mu\text{m}$  in diameter with definite outer rim and 20–30 loculi tightly arranged, each loculus 1–2  $\mu\text{m}$  in diameter; 5–6 perispiracular pores posterior to each peritreme. Abdominal spiracles in 6 pairs; inner and outer atria of posterior pair slightly smaller than other 5 pairs; each spiracle with sievelike multilocular pores present in outer atrium.

*Dorsal surface:* Densely covered in long hairlike setae, each 150–550  $\mu\text{m}$  long, scattered on head and thorax and arranged in segmental bands on abdomen, collar of each seta very small; densest vestiture on last 4 abdominal segments. Short hairlike setae, each 15–

50  $\mu\text{m}$  long, rare, scattered among long hairlike setae. Multilocular pores sievelike, each 15–16  $\mu\text{m}$  in diameter with sclerotized outer rim, with 8–30 tightly arranged, similar-sized loculi, each loculus 1–2  $\mu\text{m}$  in diameter; pores scattered among setae, more densely on midline and around margin of abdomen, especially on posterior segments; pores scattered, rare, or absent on head and thorax. Abdomen with conspicuous, elongate oval to round, raised areas of bare cuticle in a partial transverse row on each segment; distributed marginally to submarginally on abdominal segments II to IV, across entire segment on V to VIII, absent on segment IX.

*Ventral surface:* Covered in long hairlike setae (100–500  $\mu\text{m}$  long), on all body segments, densest on last 4 abdominal segments. Short hairlike setae (10–50  $\mu\text{m}$  long) scattered irregularly marginally and midventrally on abdominal segments. Sievelike multilocular pores, similar in size and structure to those on dorsum; distributed segmentally on abdomen, becoming densest near posterior abdomen and scattered, rare, or absent on head and thorax. Sternal apodemes present medially between legs of mesothoracic and metathoracic pairs. Genital opening circular with radiating fissures, situated anteriorly on segment VIII, devoid of setae and pores. Abdomen with conspicuous, elongate oval to round, raised areas of bare cuticle in a complete or partial transverse row on each of segments II to VIII.

*Description.—Cyst stage:* Body oval (2.8–5.3 mm long, 2.5–3.8 mm wide). Derm smooth. Antenna reduced to a pair of small plates, each 30–40  $\mu\text{m}$  wide, with 3–6 sensory setae. Mouthparts present; 2–3 pairs of short setae on labium; derm surrounding labium with 14–20 small peri-oral pores, each 7–10  $\mu\text{m}$  wide, with a sclerotized rim and 1–4 loculi. Thoracic spiracles well developed, each with a circular orifice to spiracular atrium; 8–12

pores arranged in 2–3 rows in atrium; atrial pores with bilocular center and outer rim of 14–18 smaller loculi. Abdominal spiracles in 6 pairs, last pair considerably smaller (about one-quarter size) than first 5; 2–3 rows of 6–12 pores each arranged around inner atrium of first 5 pairs of spiracles; last pair with 3–4 pores; pores similar in structure to those of thoracic spiracles. Cicatrices arranged around posterior abdomen in 5–7 rows of 2–8 cicatrices each; each cicatrix concave circular, 15–18 µm in diameter, 23–25 µm deep. Anal opening forming a sclerotized tube, 30 µm in diameter, with or without concentric circles of patterning on derm.

**Diagnosis.**—*Heteromargarodes* is characterized in the adult female by three features that are unique among North American genera: (i) raised bare patches on the derm, (ii) long hairlike body setae, and (iii) sievelike multilocular pores. Pores appear sievelike because they have 10–30 evenly distributed loculi, and lack the distinct outer ring of loculi found in other genera; all other North American genera have pores with a unilocular, bilocular or multilocular center and the number of central loculi rarely exceeds eight. The cyst stage of *Heteromargarodes* is characterized by peri-oral pores and numerous concave cicatrices. In both the adult female and cyst stage, *Heteromargarodes* differs from *Eumargarodes* by the number of abdominal spiracles (six pairs in *Heteromargarodes*, three pairs in *Eumargarodes*) and the cyst stage of *Heteromargarodes* has more than 10 cicatrices surrounding the anal opening whereas that of *Eumargarodes* has no more than six cicatrices.

**Distribution.**—Species of the genus *Heteromargarodes* are found in western North America and have been recorded from the states of Arizona, California, Nevada, New Mexico, and Wyoming. Species are also found in Baja California, Mexico.

**Notes.**—A redescription of this genus was part of a revision of the type species of all genera of ground pearls by Foldi (2005). At the time of Foldi’s work, *Heteromargarodes* was monotypic, but we include two other species: *H. chukar* and *H. hiemalis*.

The CSCA and the USNM collections of margarodids from the western United States have a few adult females of several other apparently undescribed ground-pearl species that share some features with species of *Heteromargarodes*, including bands of raised bare patches of cuticle, sievelike pores and papillae on the derm. The adult females of these undescribed species differ from described *Heteromargarodes* species in the number of pairs of abdominal spiracles, the number of antennal segments, and the number of loculi in the pores. There are not enough well-prepared slides available to describe these species adequately.

KEY TO SPECIES OF *HETEROMARGARODES*  
 BASED ON SLIDE-MOUNTED  
 ADULT FEMALES

- 1 Derm pores rare or absent on head and thorax; pores on anterior of body with fewer loculi (6–12) (Fig. 3G) than pores on posterior of body (18–30 loculi) (Fig. 3E). Conspicuous boss, covered with setae and pores, projecting from posterior end of abdomen (Fig. 3) . . . . . 2
- Derm pores scattered on head and thorax; locular number consistent (20–30) in pores over entire body. Boss absent (Fig. 2) . . . . . *H. chukar*
- 2 Thoracic spiracles with 18–23 sievelike multilocular pores in atrium (Fig. 1C) . . . . . *H. americanus*
- Thoracic spiracles with 8–10 sievelike multilocular pores in atrium (Fig. 3F) . . . . . *H. hiemalis*

*Heteromargarodes americanus* Jakubski  
 (Fig. 1)

*Heteromargarodes americanus* Jakubski  
 1965: 85; Foldi 2005: 513.

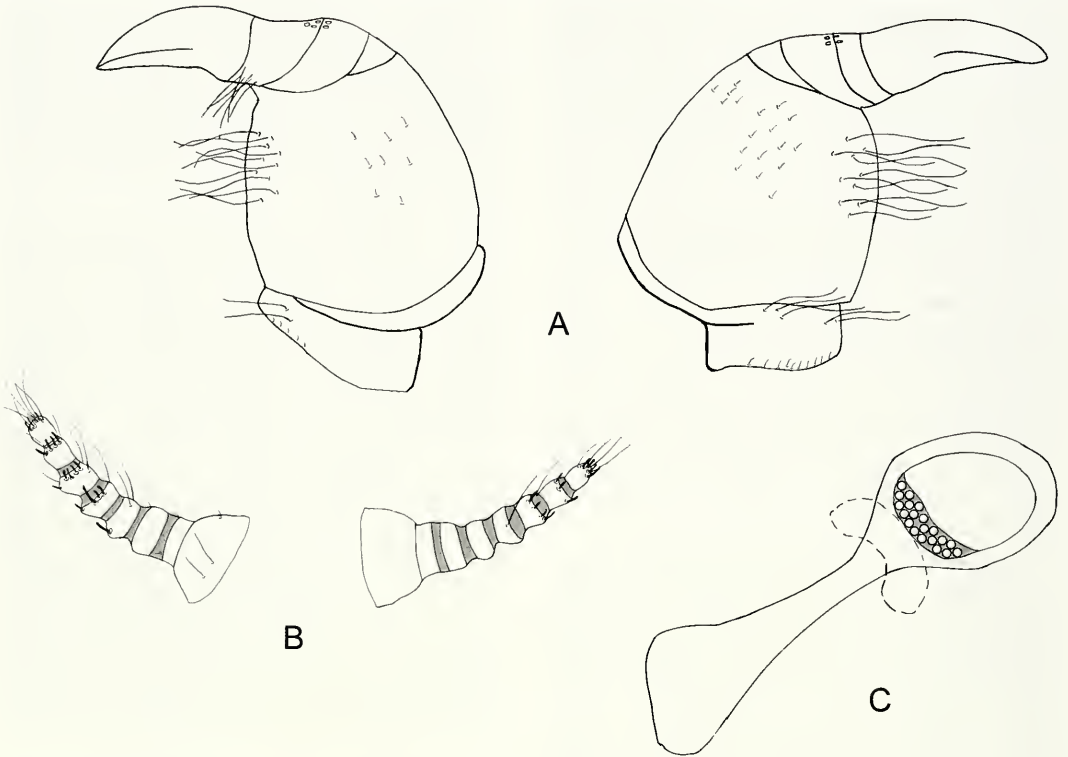


Fig. 1. Adult female of *Heteromargarodes americanus*. A, Prothoracic legs. B, Antennae. C, Thoracic spiracle.

**Description.**—*Adult female* (measurements based on lectotype and 7 specimens from Teel's Marsh, NV): Body 6.4–10.9 mm long, 6.1–10.0 mm wide; apex of abdomen with a membranous projection covered in sievelike multilocular pores and long hairlike setae (compressed and not obvious on lectotype). Antenna 580–750  $\mu\text{m}$  long. Prothoracic leg: trochanter + femur 650–1000  $\mu\text{m}$  long, 700–800  $\mu\text{m}$  in basal width; tibia and tarsus 700–1025  $\mu\text{m}$  long; claw missing on lectotype, 500–600  $\mu\text{m}$  long on non-type material; hairlike setae 200–500  $\mu\text{m}$  long on femur. Mesothoracic and metathoracic legs: trochanter + femur 900–1150 and 800–1100  $\mu\text{m}$  long, respectively; hind trochanter + femur 280–450  $\mu\text{m}$  in basal width. Anal tube diameter 40–60  $\mu\text{m}$  at opening. Thoracic spiracles including muscle plates 300–500  $\mu\text{m}$  long, 90–220  $\mu\text{m}$  wide with atrial

openings 50–100  $\mu\text{m}$  long, 65–120  $\mu\text{m}$  wide; atrium with 10–23 sievelike multilocular pores arranged in two or more rows. Abdominal spiracles with diameter of outer atria of first 5 pairs 40–60  $\mu\text{m}$ , diameter of atria of last pair 20–30  $\mu\text{m}$ ; 0–12 sievelike multilocular pores arranged around central opening into inner atrium of each spiracle, each pore 15  $\mu\text{m}$  in diameter, similar in structure to those of thoracic spiracles.

**Dorsal surface:** Long hairlike setae (250–550  $\mu\text{m}$  long) and short hairlike setae (15–30  $\mu\text{m}$  long) irregularly scattered across each segment. Sievelike multilocular pores scattered amongst setae on abdomen; pores on first 4 abdominal segments with fewer loculi (6–12) than pores on posterior abdominal segments (18–30 loculi); pores rare or absent on head and thorax, if present, similar to those on anterior abdominal segments.

*Ventral surface:* Hairlike setae (230–500  $\mu\text{m}$  long), short hairlike setae (10–30  $\mu\text{m}$  long) and sievelike multilocular pores similar in structure to those on dorsum but more densely distributed; pores rare or absent on head and thorax.

*Variation.*—We have examined material from three collections that we believe to be conspecific with the lectotype specimen of *H. americanus* and there is little variation. The only characteristics that seem to vary are the density of body setae (probably due to the size of specimens and amount of damage during slide-mounting) and the appearance of a posterior abdominal extension, or “boss” as referred to by McDaniel (1965); the angle of compression of the posterior abdomen can reduce the conspicuousness of this structure.

*Diagnosis.*—The adult female of *H. americanus* differs from that of *H. hiemalis* in its generally larger body and legs, larger thoracic spiracles with more sieve-like multilocular pores, and generally longer and denser body setae. The pores in the atrium of the thoracic spiracles of *H. americanus* form two or more rows whereas the pores of *H. hiemalis* are arranged in a single row. The long hairlike setae of *H. americanus* are 250–550  $\mu\text{m}$ , whereas the long setae of *H. hiemalis* are rarely longer than 500  $\mu\text{m}$ . The shorter setae of *H. americanus* are also, on average, longer (20–40  $\mu\text{m}$ ) than the shorter setae of *H. hiemalis* (15–30  $\mu\text{m}$ ).

*Type material.*—Lectotype (designated by Foldi 2005): ♀ of *Heteromargarodes americanus*. U.S.A., Wyoming, Powell, 24.ix.1949 (H. S. Beaudoin [sic]) (USNM). Paralectotype: cyst-stage nymph, same data as holotype (USNM). [The collector’s name, H. L. Beaudoin, is misspelled on the slide label.]

*Other material examined.*—U.S.A.: 7 ♀, Nevada, Mineral County, Teel’s Marsh [spelled Teal Marsh on label], ii.1979, on the roots of undetermined grass in a sand dune (R. J. Gill) (CSCA);

4 ♀, California, San Bernardino County, Lucerne Valley, Dead Man’s Point, 4.v.1961, in an onion field (N. Welch) (CSCA); 1 ♀, California, San Bernardino County, Victorville area, 19.v.1961, soil in onion field (N. Welch) (CSCA).

*Discussion.*—The lectotype of *H. americanus* is missing both prothoracic claws. It is difficult to distinguish the presence of a bosslike extension on the abdomen of the lectotype because it appears that area has been compressed during the slide-mounting process. Foldi (2005) published a redescription of *H. americanus* based on the lectotype slide of *H. americanus*, but his drawing of the adult female does not show the abdominal boss due to the poor quality of the specimen, nor does it include the raised bare patches present on the dorsal and ventral surfaces of the abdomen.

Ben-Dov (2005) and Foldi (2005) treated “*Deuteromargarodes americanus*” as a *nomen nudum* and claimed that it was discovered by Jakubski (1965). However, Jakubski only stated that the type slides were labeled “*Deuteromargarodes americanus*” (apparently a manuscript name), and he appropriately used the name in quotes. Thus Jakubski did not discover or create a *nomen nudum*.

In his description of the *H. americanus* cyst, (Jakubski 1965: 86) referred to the anal opening being “on top of a flat protuberance (circa 125  $\mu$ ) constructed of numerous heavily chitinized circles.” The anal opening on the paralectotype, which is the specimen that Jakubski examined, does not fit this description and it appears that he misinterpreted an abdominal spiracle as the anal area. Jakubski (1965) also described an adult male collected in Idaho in 1931 that may not be conspecific with *H. americanus*. This male was not collected with the type material or with any other material that we believe to be *H. americanus*. Jakubski expressed his uncertain-



ty concerning the identity of this specimen. Foldi (2005) referred to *H. americanus* as having bisexual reproduction, but this statement is presumably based on the questionably associated male specimen from Idaho. The mode of reproduction of *H. americanus* is thus unknown at this point. Hodgson and Foldi (2006) redescribed and illustrated this male specimen.

*Heteromargarodes hiemalis* (Cockerell),  
**new combination**

(Fig. 3)

*Margarodes hiemalis* Cockerell 1899: 416.

*Coccionella hiemalis* (Cockerell): Lindinger 1954: 615.

*Porphyrophora hiemalis* (Cockerell): Jakubski 1965: 46.

Description.—*Adult female* (measurements based on lectotype and a non-type adult female from Tucson, AZ): Body 5.0–6.6 mm long, 4.6–5.9 mm wide; apex of abdomen with a membranous projection covered in sievelike multilocular pores and long hairlike setae. Antenna 470–550  $\mu\text{m}$  long. Prothoracic leg: trochanter + femur 670–790  $\mu\text{m}$  long, 750  $\mu\text{m}$  in basal width; tibia and tarsus 700  $\mu\text{m}$  long; claw 500–530  $\mu\text{m}$  long; hairlike setae 100–500  $\mu\text{m}$  long on femur. Mesothoracic and metathoracic legs: trochanter + femur 750–990 and 730–800  $\mu\text{m}$  long, respectively; hind trochanter + femur 280–330  $\mu\text{m}$  in basal width. Anal tube diameter 45–60  $\mu\text{m}$  at opening. Thoracic spiracles including muscle plates 265–275  $\mu\text{m}$  long, 200  $\mu\text{m}$  wide, atrial openings each 50–75  $\mu\text{m}$  long, 60–90  $\mu\text{m}$  wide; atrium with 8–10 sievelike multilocular pores arranged in a single row, widening at one end. Abdominal spiracles with diameter of outer opening of first 5 pairs 50–60  $\mu\text{m}$ , diameter of atria of last pair 30–40  $\mu\text{m}$ ; 0–12 sievelike multilocular pores arranged around opening into inner atrium

of each spiracle, each pore 15  $\mu\text{m}$  diameter, similar in structure to those of thoracic spiracles.

*Dorsal surface*: Long hairlike setae (200–500  $\mu\text{m}$  long) and short hairlike setae (20–40  $\mu\text{m}$  long) irregularly scattered across each segment. Sievelike multilocular pores scattered amongst setae on abdomen; pores on first four abdominal segments with fewer loculi (6–12) than pores on posterior abdominal segments (18–30 loculi); pores rare or absent on head and thorax.

*Ventral surface*: Structure and distribution of long hairlike setae (230–500  $\mu\text{m}$  long) and sievelike multilocular pores as on dorsal surface; short hairlike setae, 20–40  $\mu\text{m}$  long, more numerous midventrally than on dorsal surface; pores rare or absent on head and thorax.

Variation.—We compared the two adult females available for study and there is little variation. The specimen from Tucson has slightly denser setae than the lectotype. The posterior boss of the female from Tucson is difficult to identify because it is compressed on the slide.

Diagnosis.—*Heteromargarodes hiemalis* is most similar to *H. americanus* [see diagnosis under *H. americanus* for a detailed comparison].

Type material.—Lectotype (here designated): adult ♀ of *Margarodes hiemalis*. U.S.A.: New Mexico, Mesilla Park, i.1899 (Cockerell) (USNM). Paralectotype: adult ♂ of *Margarodes hiemalis*, same data as lectotype (USNM). We designated the adult female from the two specimens originally described by Cockerell (1899) as the lectotype in order to preserve stability of nomenclature for this species.

Other material examined.—1 adult ♀ and 1 cyst-stage nymph (same slide), Arizona, 30 mi [48 km] south of Tucson, Santa Rita Experimental Range, xii.1978, ex *Prosopis* (E. Hoffman) (CSCA).

Discussion.—Jakubski (1965) placed *M. hiemalis* in *Porphyrophora*, but in the most recent revision of that genus, Vahedi (2002) did not include *M. hiemalis* because it is found in North America. *Heteromargarodes* and *Porphyrophora* have similar hairlike setae covering the body, but differ in the number of abdominal spiracles, antennal shape and sensory structures. McDaniel (1965, 1966) described “tooth-like structures” on the foreleg claw of *M. hiemalis*, but these structures were not apparent on the lectotype or the other specimen that we considered as conspecific.

(Cockerell 1899: 416) described the adult female of *M. hiemalis* as: “Bright lemon yellow, very soft, oval; 5.5 mm. long, 4 broad, 2.5 high; segmentation distinct, each segment with a whorl of mostly blackish but inconspicuous hairs; apex of abdomen with a small reddish hairy prominence;...” This contrasts with La Rivers (1967) description of *M. chukar* (see below). In his original description, Cockerell described walking up a path and seeing male scales “hurrying to and fro.” He then watched as one of them started digging, almost completely burying itself. Cockerell dug after it and discovered a “plump yellow female coccid” (1899: 415). He explained that the purpose of a thickened femur on the anterior pair of legs in males of *Margarodes* spp. was unknown until he witnessed the male of *M. hiemalis* digging with its enlarged fossorial prothoracic legs.

*Heteromargarodes chukar* (La Rivers),  
**new combination**  
 (Fig. 2)

*Margarodes chukar* La Rivers 1967: 4.

Description.—*Adult female* (based on 5 slide-mounted paratype specimens): Body 3.8–10.0 mm long, 3.0–8.4 mm wide; apex of abdomen rounded, without a membranous projection. Antenna 450–

800  $\mu\text{m}$  long. Prothoracic leg: trochanter + femur 350–800  $\mu\text{m}$  long, 400–600  $\mu\text{m}$  in basal width; tibia + tarsus 360–900  $\mu\text{m}$  long; sclerotized claw 380–650  $\mu\text{m}$  long; hairlike setae 200–500  $\mu\text{m}$  long on femur. Mesothoracic and metathoracic legs: trochanter + femur 550–1180  $\mu\text{m}$  and 500–1100  $\mu\text{m}$  long, respectively; hind trochanter + femur 180–450  $\mu\text{m}$  in basal width. Anal tube diameter 30–50  $\mu\text{m}$  at opening. Thoracic spiracles including muscle plate 180–350  $\mu\text{m}$  long, 50–100  $\mu\text{m}$  wide, atrial opening 120  $\mu\text{m}$  long, 80  $\mu\text{m}$  wide; atrium with 6–10 sievelike multilocular pores; each pore 10–12  $\mu\text{m}$  in diameter with definite outer rim and 20–30 tightly arranged loculi, each loculus 1–2  $\mu\text{m}$  in diameter, pores in a single row, number of pores increasing at one end. Abdominal spiracles in 6 pairs; outer opening of 5 anterior pairs 40–70  $\mu\text{m}$  in diameter with 0–8 sievelike multilocular pores, outer opening of posterior pair 20–30  $\mu\text{m}$  in diameter with 6–8 sievelike multilocular pores; pores 9–10  $\mu\text{m}$  in diameter, arranged around central opening into inner atrium; pores similar to those of thoracic spiracles.

*Dorsal surface*: Long hairlike setae (250–550  $\mu\text{m}$  long); short hairlike setae (20–40  $\mu\text{m}$  long) rare, irregularly scattered. Sievelike multilocular pores with 20–30 tightly arranged loculi found on head, thorax and abdomen.

*Ventral surface*: Structure of long hairlike setae (230–500  $\mu\text{m}$  long), short hairlike setae (20–40  $\mu\text{m}$  long) as on dorsum, setae more dense on venter than dorsum; sievelike multilocular pores as on dorsal surface; pores scattered amongst setae on head, thorax and distributed segmentally on abdomen.

Variation.—We examined paratypes and other specimens that we believe to be conspecific with the paratypes. We noted variation in the body size of adult females, even within a single collection, and density of setae varies among collections, rather than among specimens

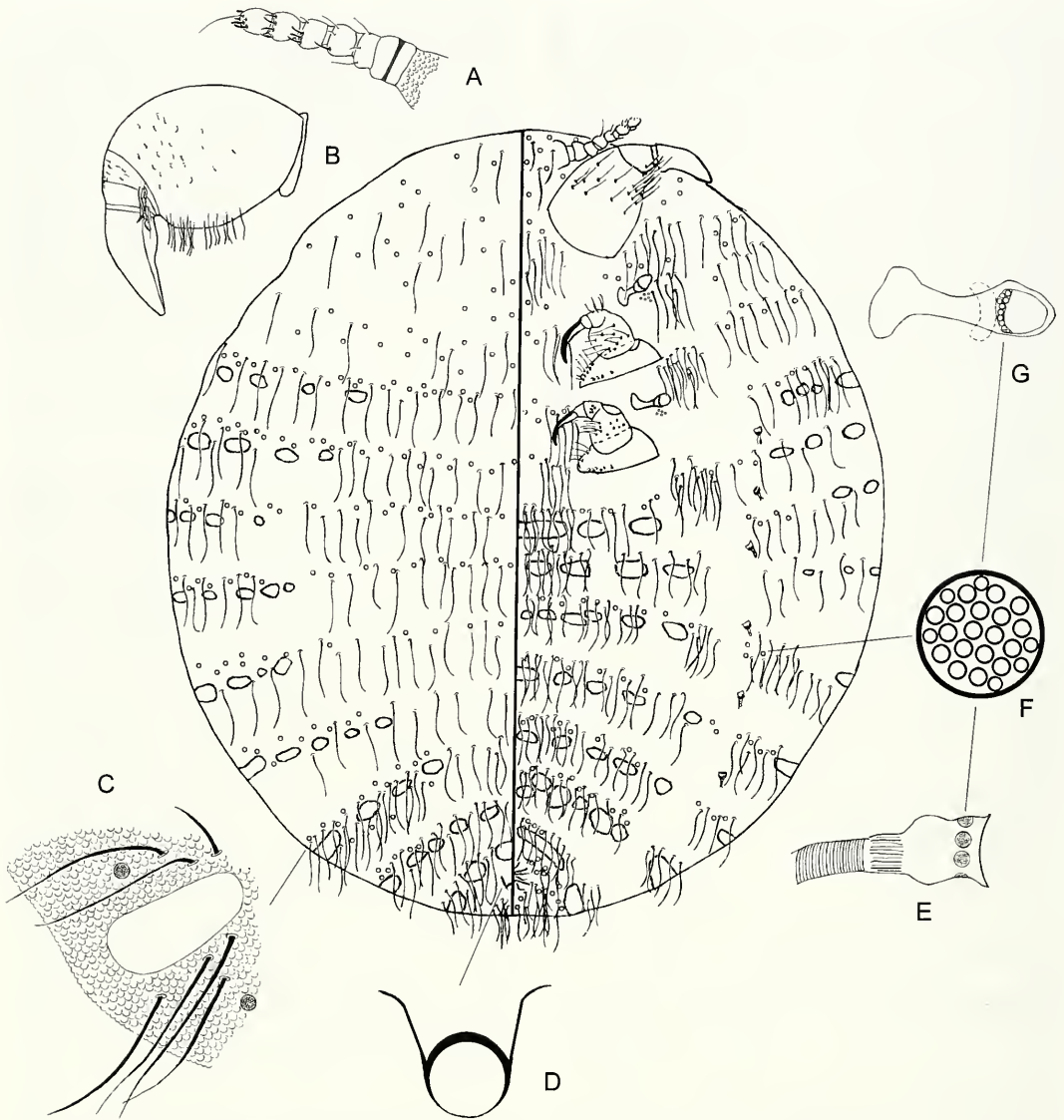


Fig. 2. Adult female of *Heteromargarodes chukar*. A, Dorsal surface of antenna. B, Dorsal surface of prothoracic leg. C, Derm enlargement. D, Anal opening. E, Abdominal spiracle. F, Multilocular pore. G, Thoracic spiracle.

of different sizes. The large adult female from Mexico is covered with very dense setae and both large and small adult females from Red Rock Canyon have many fewer setae than the Mexican specimen.

**Diagnosis.**—The adult female of *H. chukar* differs from that of *H. hiemalis* and *H. americanus* by the absence of a conspicuous boss projecting from the

posterior end of the abdomen and by the presence of pores on the head and thorax. All derm pores found in *H. chukar* have a consistent number of loculi (20–30) as opposed to the varying numbers on anterior versus posterior abdomen found in *H. hiemalis* and *H. americanus*.

**Type material.**—Paratypes of *Margarodes chukar*: 5 adult ♀, U.S.A.: Nevada,

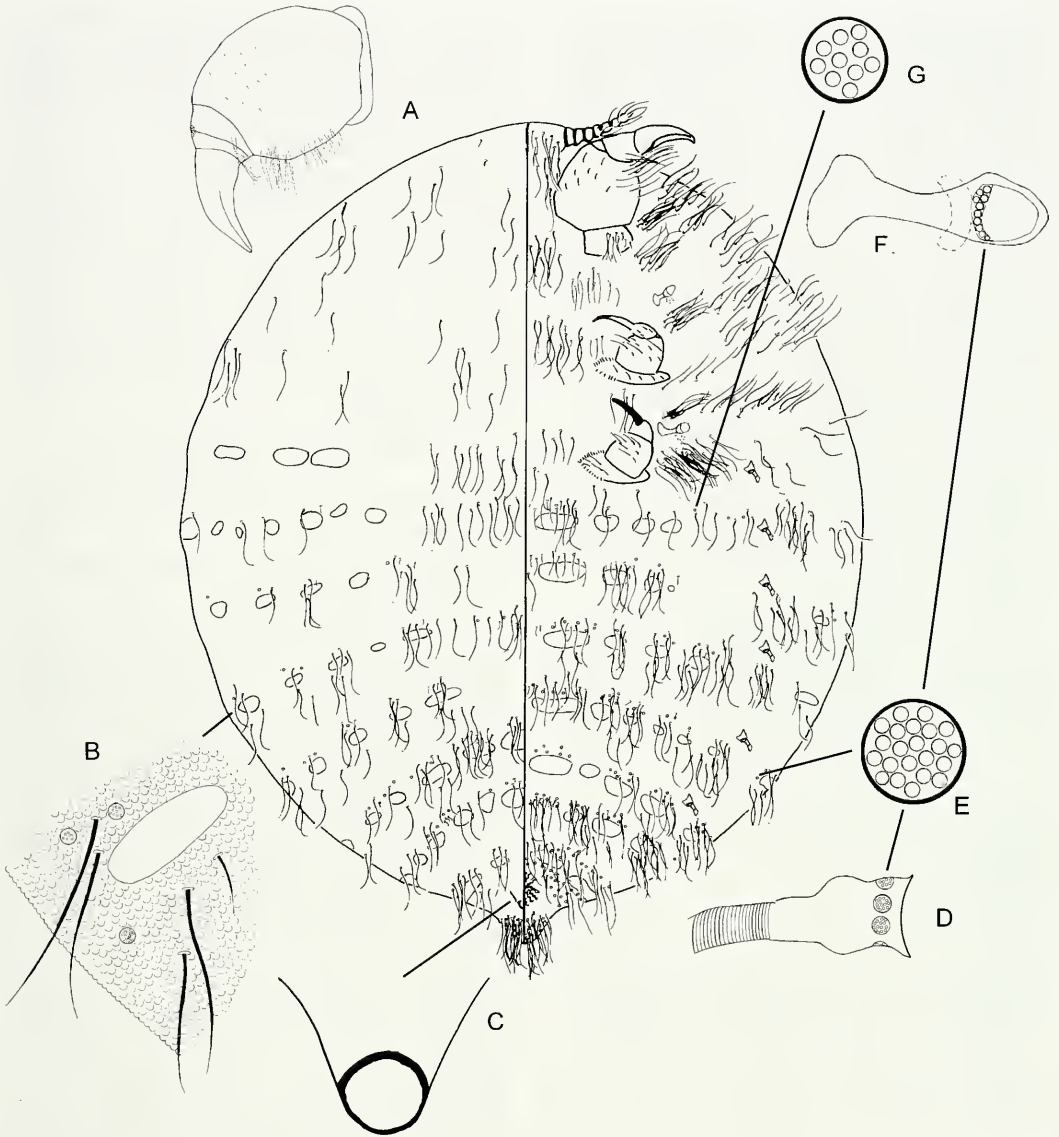


Fig. 3. Adult female of *Heteromargarodes hiemalis*. A, Dorsal surface of prothoracic leg. B, Derm enlargement. C, Anal opening. D, Abdominal spiracle. E, Multilocular pore found in spiracles and on posterior abdomen. F, Thoracic spiracle. G, Multilocular pore found on anterior abdomen.

Washoe County, Red Rock Canyon, 26.ix.1964, in crop of chukar *Alectoris graeca* (L. Bouy and D. Savage) (CSCA). The above material is part of La Rivers' original collection because the collection data precisely match those given in the original description, except that the name of one of the collectors, Laun

Bouy, apparently is misspelled as "Bouy" on the slide labels. These five specimens were prepared as microscope slides by R. F. Wilkey, who worked at the CDFA at that time (R. J. Gill, personal communication). No other original specimens of this species could be found at the collection of the Nevada Department

of Agriculture, where La Rivers material might have been deposited. The entomologist responsible for that collection was uncertain of the depository of La Rivers' specimens of *M. chukar* and suggested that they may have been lost after his death (J. B. Knight, in litt.). We here treat the five slides held at the CSCA as paratypes because the original description clearly says that there was "a type and a large number of paratypes (all females)" (La Rivers 1967: 6) and the measurements given in the original description are for the "type" only. Even though La Rivers probably did not see Wilkey's slide-mounted females, he presumably sent the specimens to Wilkey from his type series. The holotype appears to be lost.

Other material examined.—U.S.A.: 7 ♀, Nevada, Washoe County, Leadville, 25.ix.1963, being carried to the nest by *Pogonomyrmex salinus* (R. C. Bechtel) (CSCA). MEXICO: Baja California, 5 mi [8 km] N of Guerrero Negro, 14.iv.1991, on the coastal sand dunes below *Senecio* sp. (G. R. Ballmer) (CSCA).

Discussion.—The original specimens of *M. chukar* were discovered in eastern Nevada in the crop of the partridge *Alectoris chukar* (originally called *Alectoris graeca* by La Rivers), commonly called the chukar. The main diet of the chukar in the fall is cheatgrass (*Bromus tectorum*) (Walter and Reese 2003), but no ground pearls were found on that plant, although it was prominent in the location where the chukars were found. (La Rivers 1967: 4) described the body of the adult female as: "color white; body oval, moderately beset with long white hairs of setae; segmentation evident on all sides; length of preserved type 9 mm., width 7 mm." He said that the specimens were alive when taken from the crops of the chukars, and thus the color given in his description may be that of living adult females. However, he may have

been describing the color of preserved females, since his description was published nearly three years after the collection of the specimens. Cockerell (1899) described the adult female of the *M. hiemalis* as bright lemon yellow (see above under that species). LaRivers (1967) pointed out in his description of *M. chukar*, that when using McDaniel's (1966) key, *M. chukar* will key to *M. hiemalis*, but the difference between the two species is that *M. chukar* lacks an abdominal boss.

*Eumargarodes laingi* Jakubski

*Eumargarodes laingi* Jakubski 1950: 397;  
Jakubski 1965: 49.

*Margarodes dactyloides* McDaniel 1966:  
237. **New synonym.**

The holotype of *Margarodes dactyloides* McDaniel is a slide-mounted adult female that has a damaged posterior abdomen and the slide-mount is poor. The paratypes (immature specimens) that McDaniel (1966) mentioned in his original description could not be located in any of the institutions that are known to house McDaniel's material (see below). Examination of the holotype reveals that *M. dactyloides* is identical to Jakubski's concept of *Eumargarodes laingi*. It has the following diagnostic characteristics of *E. laingi*: three pairs of abdominal spiracles, multilocular pores with 6–8 loculi arranged in a circle, and derm with sparse hairlike setae that taper to a point. In the original description, McDaniel (1966) described the abdomen of the holotype of *M. dactyloides* as having a "conspicuous stout boss broadly curved at the apex and devoid of any hair-like setae and multilocular pores." This structure appears to be the everted vulvar area. Based upon examination of the type material of *M. dactyloides* and material from the type locality of *E. laingi*, we synonymize *M. dactyloides* with *E. laingi*.

Type material.—Holotype ♀ of *Eumargarodes laingi*. AUSTRALIA: Queensland, Bundaberg, Nov. 1938, on sugarcane roots, R. W. Mungomery (BMNH). This slide was not examined for the present work, but we examined 2 adult female specimens of *E. laingi* that were slide-mounted by P. J. Gullan and compared with the holotype of *E. laingi* by P. J. Gullan in 1983. These slides have the following data: AUSTRALIA: 2 ♀, Queensland, Bundaberg, Qunaba area, Burnett Heads Road, Jorgansen Bros, 15.viii.1972, ex sugar cane - second ratoon crop (R. M. Bull) (ANIC).

Holotype ♀ of *Margarodes dactyloides*. U.S.A.: Texas, Scotland, North on Highway 281, on *Buchloe dactyloides*, 21.vi.1965 (S. McDaniel and B. McDaniel) (USNM). McDaniel stated in the original description that the holotype was deposited in the USNM collection and paratypes were kept in McDaniel's personal collection. The USNM had no record of the slide in their collection, and McDaniel's personal collection was deposited at the museum at Texas A&M in College Station, Texas, whereas remnants of a teaching collection were left at South Dakota State University (SDSU) in Brookings, South Dakota. The holotype slide appeared to be lost because it could not be located initially when we contacted the latter institutions, but was discovered in an old slide store box at the Insect Research Collection at SDSU by Dr. Paul Johnson, and now has been deposited in the USNM. Unfortunately, the paratypes from McDaniel's personal collection have not been found.

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